

B R E V I O R A

Museum of Comparative Zoology



US ISSN 0006-9698

CAMBRIDGE, MASS.

22 JUNE 2018

NUMBER 562

***EUSTHENOPTERON JENKINSI* SP. NOV. (SARCOPTERYGII, TRISTICHOPTERIDAE) FROM THE UPPER DEVONIAN OF NUNAVUT, CANADA, AND A REVIEW OF *EUSTHENOPTERON* TAXONOMY**

JASON P. DOWNS,^{1,2} EDWARD B. DAESCHLER,² ALISON M. LONG,¹ AND NEIL H. SHUBIN³

ABSTRACT. New material from the Upper Devonian (Frasnian) Fram Formation of Ellesmere Island, Nunavut, Canada, represents a new large-bodied species of *Eusthenopteron*. The complete and well-preserved nature of the fossil material enables a description of anatomy that is otherwise poorly represented in most *Eusthenopteron* species: this includes braincase (ethmosphenoid and otic-occipital), scapulocoracoid, and pectoral fin. The new species is distinguished from other *Eusthenopteron* species by its large body size, pitted rather than tuberculated dermal cranial ornament, a distinct caudolateral margin of the vomer, an unossified basicranium, and a horizontally oriented hyomandibula. A large sample size and decades of detailed study of *Eusthenopteron foordi* have resulted in an important anatomical understanding of that species, but a lack of autapomorphies has complicated efforts to diagnose the grouping *Eusthenopteron*. We review the taxonomic history of *Eusthenopteron* and provide a new diagnosis that relies on a combination of discrete features that are commonly preserved and unaffected by specimen quality.

KEY WORDS: Sarcopterygii; Tristichopteridae; Fram Formation; Late Devonian; Frasnian

INTRODUCTION

We report on new material representing the tristichopterid taxon *Eusthenopteron* (Whiteaves, 1881) from the Upper Devonian (Frasnian) Fram Formation. The material was collected at the NV2K17 locality, Ellesmere Island, Nunavut, Canada (Fig. 1), a site that has produced a diverse assemblage of vertebrates since its discovery in 2000. The NV2K17 fauna includes asterolepid antiarchs, a dipnoan, two holoptychiid porolepiforms (*Laccognathus embryi*,

¹ Delaware Valley University, Department of Biology, Doylestown, Pennsylvania 18901, U.S.A.; e-mail: jason.downs@delval.edu, longa0936@delval.edu

² Academy of Natural Sciences of Drexel University, Department of Vertebrate Biology, 1900 Benjamin Franklin Parkway, Philadelphia, Pennsylvania 19103, U.S.A.; e-mail: ebd29@drexel.edu.

³ University of Chicago, Department of Organismal Biology and Anatomy, 1027 E 57th Street, Chicago, Illinois 60637, U.S.A.; e-mail: nshubin@uchicago.edu

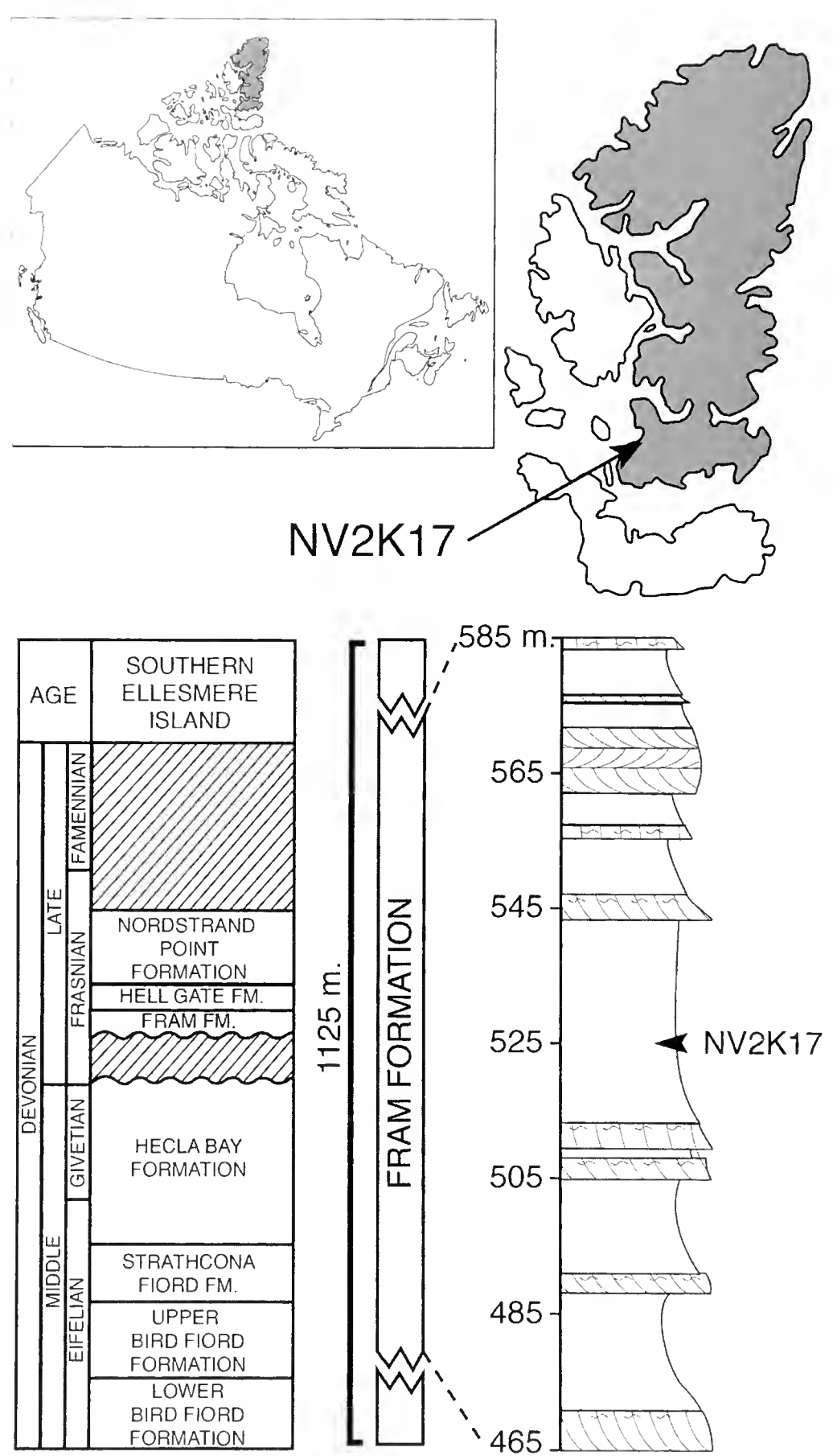


Figure 1. Map of Ellesmere Island showing the location of NV2K17 site (top), stratigraphy of the Okse Bay Group (bottom left) and stratigraphy of the Fram Formation type section (bottom right).

Downs et al., 2011, and *Holoptychius bergmanni*. Downs et al., 2013), osteolepidids, and the elpistostegalian *Tiktaalik roseae* (Daeschler et al., 2006; Shubin et al., 2006; Downs et al., 2008). *Eusthenopteron* is

perhaps the best understood tristichopterid, owing in large part to the anatomically complete specimens of *Eusthenopteron foordi* from the Miguasha locality of Quebec and Jarvik's (e.g., 1942, 1944a, 1944b, 1954,

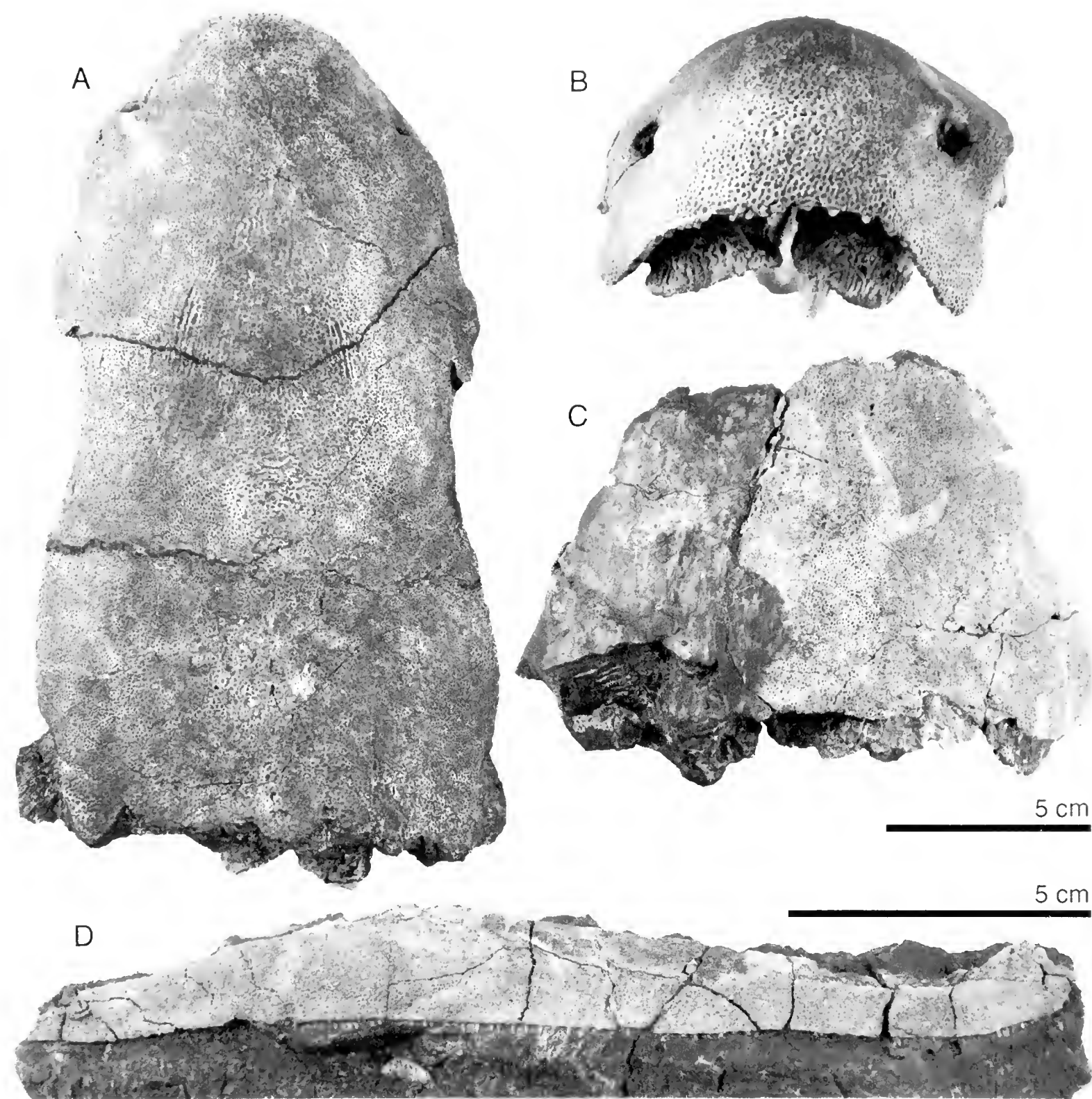


Figure 2. *Eusthenopteron jenkinsi* sp. nov. A. NUFV 1245, parietal shield in dorsal view; B. NUFV 1245, parietal shield and associated vomers in rostral view; C. NUFV 1187, postparietal shield in dorsal view; D. NUFV 1199, right maxilla in lateral view. Upper scale bar applies to A, B, and C; lower scale bar applies to D.

1980, 1996) work to describe this anatomy in detail. The grouping has been additionally represented by five species distributed among England (*Eusthenopteron farloviensis*, White, 1961), Latvia (*Eusthenopteron sāve-söderberghi*, Jarvik, 1937; *Eusthenopteron obruchevi*, Vorobyeva, 1977), Russia (*Eusthenopteron* [=Jarvikina, Vorobyeva, 1977] *wenjukowi*

[Rohon, 1889]), and Scotland (*Eusthenopteron traquairi*, Westoll, 1937). The NV2K17 sample of *Eusthenopteron* discussed here includes well-preserved hyomandibulae, lower jaws, ethmosphenoids and otic-occipital with associated skull roof and dermal palate, clavicles and cleithra with associated scapulocoracoid, and fin bones

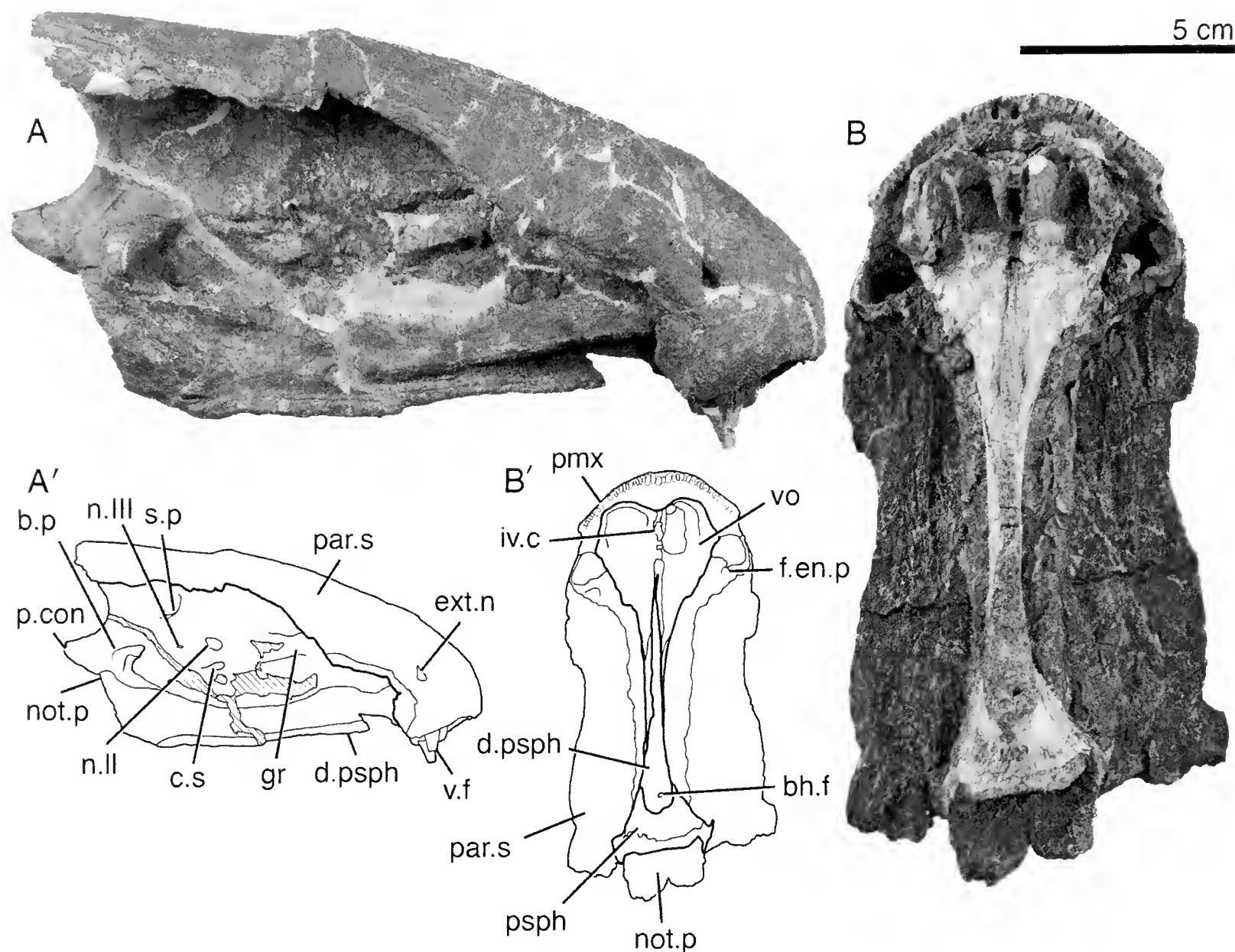


Figure 3. *Eusthenopteron jenkinsi* sp. nov. A, NUFV 1201, ethmosphenoid and associated parietal shield in right lateral view (A', labeled illustration); B, NUFV 1245, dermal palatal elements and associated ethmosphenoid and parietal shield in palatal view (B', labeled illustration). Abbreviations: bh.f, buccohypophysial foramen; b.p, basipterygoid process; c.s, possible contact site for the palatoquadrate; d.psph, denticulated field of the parasphenoid; ext.n, external naris; f.en.p, fenestra endonarina posterior; gr, groove that may accommodate the origin of the levator bulbi muscle; iv.c, intervomerine canal; n.II, foramen for cranial nerve II; n.III, foramen for cranial nerve III; not.p, notochord pit; par.s, parietal shield; p.con, processus connectens; pmx, premaxilla; psph, parasphenoid; s.p, suprapterygoid process; v.f, vomerine fang; vo, vomer.

including humerus, radius, and ulna. Other potentially relevant Fram Formation sarcopterygian fossils were collected by Per Schei during the Norwegian Second Fram Expedition of 1898–1902 on southwestern Ellesmere Island, near the head of Goose Fiord. This material, described by Kiaer (1915), includes sarcopterygian teeth (PMO A13054, A13180, A13213, A13220; see the Institutional Abbreviations paragraph at the end of this section), ridged scales (PMO

A13195, A13201, A13202, A13304) originally assigned to *Glyptolepis* cf. *paucidens* and “*Holoptychius scheii*” (and later reassigned to *Glyptolepis* sp. indet. [Ørvig, 1957] and *Holoptychiidae* indet. [Downs et al., 2011], respectively) and a “badly preserved” “fragment of a jaw” (PMO A13209) that was originally assigned to “*Holoptychius scheii*” (Kiaer, 1915:48) and later reassigned to *Holoptychius* sp. indet. by Ørvig (1957). The taxonomic assignment of the “jaw”

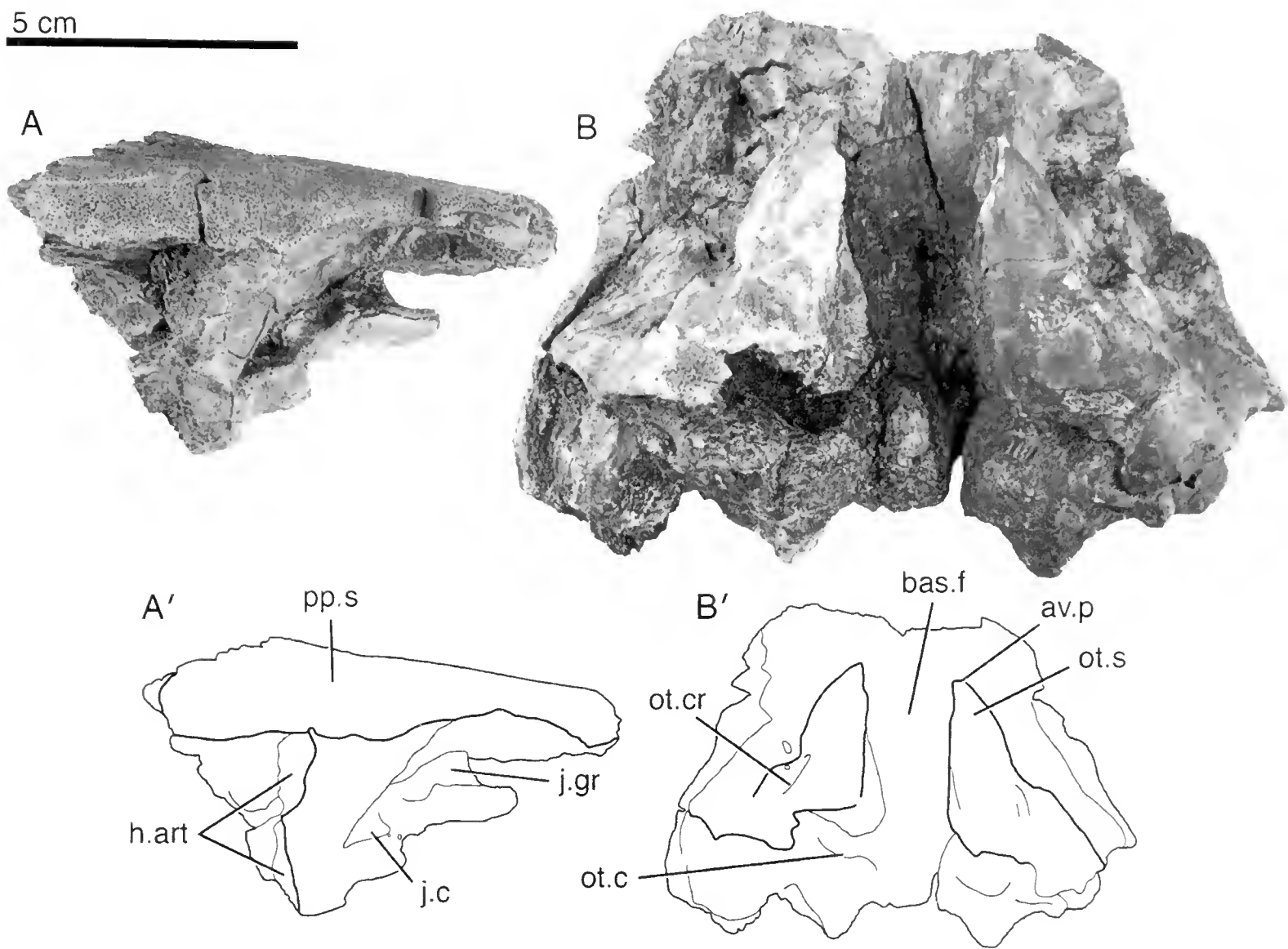


Figure 4. *Eusthenopteron jenkinsi* sp. nov., NUFV 1187, otic-occipital and associated postparietal shield in (A) right lateral view (A', labeled illustration) and (B) ventral view (B', labeled illustration). Abbreviations: av.p, anteroventral articular process; bas.f, basiscranial fenestra; h.art, hyomandibula articulation site; j.c, jugular canal; j.gr, jugular groove; ot.c, otic capsule; ot.cr, ventral otic crest; ot.s, otic shelf; pp.s, postparietal shield.

specimen was made by size matching, given the known Fram Formation fauna at that time. A new study of PMO A13209 (Kiaer, 1915, pl. VIII, fig. 5) by one of us (EBD) confirms that the specimen is a short section of palate including maxilla, ectopterygoid, and entopterygoid. The ectopterygoid shows a single, nearly linear row of tooth positions that includes a fang pair and smaller teeth mesial and distal to it. With this organization of teeth, the specimen is not visually consistent with the two known holoptychiids from the Fram Formation, *H. bergmanni* (Downs et al., 2013) and *L. embryi* (Downs et al., 2011). Although more likely to

represent a tristichopterid than a holoptychiid, and perhaps even belonging to the species described below, the absence of diagnostic features in PMO A13209 leads us to a conservative assignment of *Sarcopterygii* indet.

The recent Nunavut Paleontological Expeditions (1999–2014) have made substantial additions to the Fram Formation vertebrate faunal list. The material we present here represents the first tristichopterid species to be described from the Fram Formation and one of the most anatomically complete species of *Eusthenopteron*.

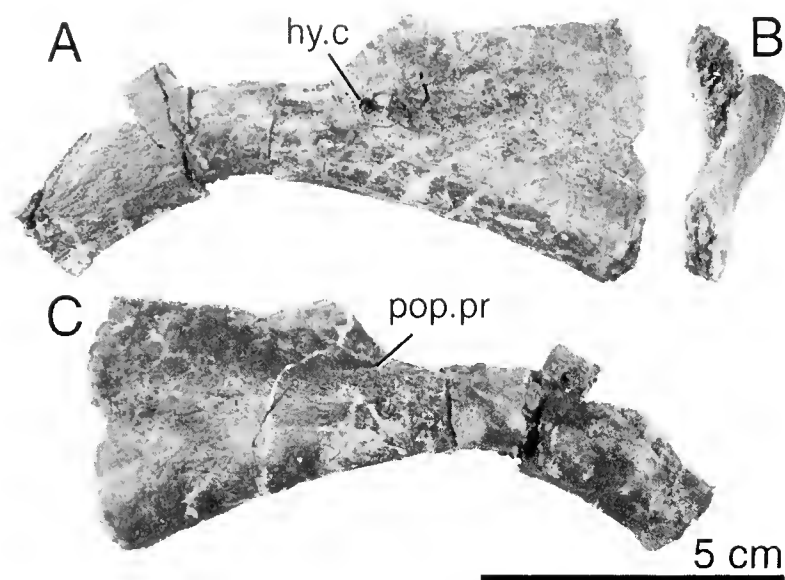


Figure 5. *Eusthenopteron jenkinsi* sp. nov., NUFV 1186, hyomandibula in (A) medial, (B) proximal, and (C) lateral views. The proximal view (B) shows dorsal and ventral attachment sites for the lateral commissure. Abbreviations: hy.c, jugular canal; pop.pr: preopercular process.

Geological Setting. The Fram Formation belongs to the Okse Bay Group (Fig. 1), the upper part of the Middle to Upper Devonian clastic wedge of Arctic Canada's Franklinian Geosyncline (Mayr, 1994). There are five formations in the Okse Bay Group: Strathcona Fiord, Hecla Bay, Fram, Hell Gate, and Nordstrand Point (Embry and Klovan, 1976). The sediments of the Okse Bay Group were shed into a foreland basin from three sources: the Ellesmerian Orogenic Belt to the north and the Caledonian Orogenic Belt and the Precambrian Shield, both to the east (Embry, 1988). Scotese and McKerrow (1990) provide a paleogeographic reconstruction that places the Ellesmerian Orogenic Belt in northern Laurussia (Euramerica), an equatorial landmass in the Middle to Late Devonian Period.

All the new tristichopterid fossils were collected at the NV2K17 locality within the type section of the Fram Formation. NV2K17 is on southern Ellesmere Island, close to the east arm of Bird Fiord, in the southward-dipping limb of the Schei Syncline. Palynological data support an early–

middle Frasnian age (Chi and Hills, 1976; Embry and Klovan, 1976). The Fram Formation represents meandering river and floodplain facies and alternates between siltstones representing overbank deposits and resistant sandstones representing channel and point bar deposits (Embry and Klovan, 1976). These are organized into fining upward cycles, each of which is about 10–15 m thick (Fig. 1; Embry and Klovan, 1976; Embry, 1991). The productive zone of the NV2K17 locality, approximately 20 cm thick, is interpreted to be the product of a single channel avulsion event during which suspended load and vertebrate remains were quickly deposited and buried on the floodplain (Miller et al., 2007). This interpretation is supported by a taphonomic context, wherein there is no size sorting or preferred orientation within the bone bed (Miller et al., 2007).

Institutional Abbreviations. AM, AMF, Australian Museum, Sydney; ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.; MNHN.F.ARD, Ardennes Fossil Collection, Muséum National d'Histoire Naturelle, Paris, France; NUFV, Nunavut Fossil Vertebrate Collection, Canadian Museum of Nature, Ottawa; P., Geological Museum, University of Copenhagen, Denmark; PMO, Natural History Museum, University of Oslo, Norway; PMU, Museum of Evolution, Uppsala University, Sweden; RMSE, Royal Museum of Scotland, Edinburgh.

SYSTEMATIC PALEONTOLOGY

Sarcopterygii Romer 1955
 Osteolepiformes Berg 1937
 Tristichopteridae Cope 1889
Eusthenopteron Whiteaves 1881

Type Species. *Eusthenopteron foordi* Whiteaves 1881.

Revised Diagnosis. *Eusthenopteron* is diagnosed by the combination of two fang pairs on the third coronoid and no fang pair on the dentary.

Remarks. *Eusthenopteron* is a grouping of Givetian to Frasnian tristichopterid tetrapodomorphs that includes the following seven species: *E. farloviensis* (England), the type species *E. foordi* (Canada), *E. obruchevi* (Latvia), *E. säve-söderberghi* (Latvia), *E. traquairi* (Scotland), *E. wenjukowi* (Russia), and the new species from Canada that is presented below.

Vorobyeva (1977) named a new monotypic genus and rediagnosed *Eusthenopteron wenjukowi* as *Jarvikina wenjukowi*. She distinguished *Jarvikina* from *Eusthenopteron* using the following list of features: “contact between posterior supraorbital and intertemporal,” “further back” position of the pineal complex, “relatively short” otic-occipital and “longer” cheek, “long” maxilla with height increasing caudally, height of lacrimal “about the same” at rostral and caudal margins of the orbit, “a greater overlap of the scales,” “short quadrate,” and dentine in the teeth with “many folds” (translated from Vorobyeva, 1977:182). Only one of *Jarvikina*’s distinguishing features, supraorbital-intertemporal contact, does not rely on relative or subjective language, but this contact is present in *Eusthenopteron*, including the type species (RMSE 1897-51-204; Jarvik, 1980). The validity of *Jarvikina* has been questioned since the time of its publication; Jarvik (1980) himself continued to use the combination *E. wenjukowi* despite noting Vorobyeva’s (1977) use of the name *Jarvikina*. The new material from Ellesmere Island extends the size and shape variation exhibited by *Eusthenopteron*, further diminishing the uniqueness of *E. wenjukowi*. Thus, in this paper, we have chosen to use the combination *E. wenjukowi*.

Our revised diagnosis for *Eusthenopteron* is based on a combination of features. Autapomorphies have not been identified for *Eusthenopteron* or for the type species *E. foordi*. The history and ongoing issues of *Eusthenopteron* taxonomy are described further in the Discussion section of this paper.

Eusthenopteron jenkinsi sp. nov.

tristichopterid sarcopterygian Daeschler et al., 2006

cf. *Eusthenopteron* sp. Downs et al., 2011

tristichopterid Downs et al., 2013

undescribed tristichopterid, Shubin et al., 2015

Etymology. The name *Eusthenopteron* (from the Greek *eusthenes*, stout, and *pteron*, fin) refers to the pterygiophores of the second dorsal and anal fins. The species is named in honor of the late Dr. Farish A. Jenkins, Jr., of Harvard University and the Museum of Comparative Zoology, for his central role in the Nunavut Paleontological Expeditions from 1999 to 2008. He was a key contributor to the anatomical research, the fieldwork, and the quality of life in camp.

Holotype. NUFV 1187, humerus and skull including parietal shield, ethmosphenoid, dermal palatal elements, postparietal shield, and otic-occipital.

Type Locality and Horizon. NV2K17 locality (77°09′59.1″N, 86°16′9.42″W), Fram Formation near the eastern arm of Bird Fiord on southern Ellesmere Island, Nunavut Territory, Canada. Palynological data indicate an early Frasnian age (*medius* and *maclarenii* zones of Chi and Hills, 1976).

Referred Materials. NUFV 671, 1178, 1182, 1185, 1246, partial or complete mandible; 1057, 1186, hyomandibula; 1179, fin mesomere; 1180, 1181, ulna; 1183, scapulo-coracoid; 1184, radius; 1186, hyomandibula; 1187 (holotype), skull roof, ethmosphenoid, dermal palatal elements, otic-occipital, and humerus; 1196, partial cleithrum; 1197, 1206

clavicle; 1199, maxilla; 1200, humerus; 1201, 1245, parietal shield, ethmosphenoid and dermal palatal elements; 1202, two partial cheek elements; 1203, 1198, cleithrum and scapulocoracoid; 1204, palatal fragments.

Diagnosis. Tristichopterid referred to *Eusthenopteron* by the combination of two fang pairs on the third coronoid and no fang pair on the dentary. It is distinguished from previously described *Eusthenopteron* species by exhibiting the following anatomical features: large body size (estimated body length from referred materials is approximately 2.1 m), pitted rather than tuberculated ornament on the dermal skull bones, a distinct corner along the caudolateral margin of the vomer, vertical orientation of the lateral commissure's hyomandibula articulation and corresponding horizontal orientation of the hyomandibula, and unossified basicranium.

DESCRIPTION

Gross Cranial Morphology and Ornament. The preserved skull roof of *Eusthenopteron jenkinsi* suggests a long snout and torpedo-shaped skull for the species (Fig. 2). The maximum width-to-length ratio of the parietal shield in dorsal view is 0.54 (NUFV 1245; Fig. 2A) and is comparable then to the same ratios calculated for *E. foordi* (~0.52 in P.33, Jarvik, 1944a:33) and *E. säve-söderberghi* (~0.57 in the holotype PMU 22990 [=P.1020 of Jarvik, 1944a]). In *E. jenkinsi*, the ratio of parietal shield length to postparietal shield length (1.85 in the holotype) is also typical for species of *Eusthenopteron* (between 1.7 and 1.95 for *E. foordi*, *E. säve-söderberghi*, and *E. traquairi*; Bishop, 2013). This indicator of snout length has been used to differentiate between the species of *Eusthenopteron* and those of *Tristichopterus*, whose parietal shield is relatively shorter (1.4–1.57; Jarvik, 1937; Westoll, 1937; Bishop, 2013). The skull shape of *Eusthenopteron* species is unlike the wide head and blunt

snout of *Cabonnichthys burnsi* (Ahlberg and Johanson, 1997), *Eusthenodon wängsjöi* (Jarvik, 1952), and *Hyneria lindae* (Daeschler and Downs, 2018) and also different from the narrow head and “acutely pointed snout” of *Mandageria fairfaxi* (Johanson and Ahlberg, 1997:47).

All parietal and postparietal shield specimens of *E. jenkinsi* are associated with the ossified ethmosphenoid and otic-occipital, respectively. Most *Eusthenopteron* species with preserved cranial material exhibit an ossified braincase. This includes *E. foordi* (Jarvik, 1980), *E. obruchevi* (Vorobyeva, 1977), and *E. säve-söderberghi* (Jarvik, 1937). Notably, no ossified braincase material is known for *E. traquairi* and this is despite the fact that the holotype preserves the parietal shield in visceral view. *Eusthenopteron jenkinsi* is unique among the species of *Eusthenopteron* in that the basicranium is unossified. This creates a ventral exposure of the internal otic capsules and cranial cavity.

The ornament of the *E. jenkinsi* skull roof (Fig. 2B) is very different from the rounded tubercles observed in *E. foordi* (Jarvik, 1944a), *E. säve-söderberghi* (Jarvik, 1937), and *E. traquairi* (Westoll, 1940). The skull roof is pitted rather than tuberculated and is otherwise smooth at the surface. Pits in the tristichopterid skull roof have been shown to communicate with a complex network of sensory tubules within the skull (Jarvik, 1944a; Daeschler and Downs, 2018). Jarvik's (1944a) sectioning of the *E. foordi* skull revealed that these branching sensory tubules connect to parasagittal linear sensory canals running through the skull roof. According to Jarvik (1944a), the linear canals extend the length of the skull from premaxilla to lateral extrascapular. Subsurface sensory tubules and canals may be present but are not yet observable in the *E. jenkinsi* sample.

Parietal Shield. The parietal shield is known from three specimens (NUFV 1187, 1201, 1245 [Figs. 2A, B]), all of which are obscured viscerally by the attached ethmosphenoid. The only portion of the orbital margin that is known for *E. jenkinsi* is the anterior supraorbital, so the shape of the orbit remains unknown. The external nares of *E. jenkinsi* are large and circular (Fig. 2B). They are situated on the rostral surface of a lateral bulge in the parietal shield and therefore face distinctly rostrally rather than laterally. Contacts among the elements of the parietal shield are not visible, but the pattern of ornament reveals the rostral border of the parietals and the contact between parietals and median postrostral. In dorsal view of an articulated specimen (NUFV 1187), the rostral border of the parietals and the caudal border of the median postrostral both fall within the orbital margin. The width-to-length ratio of the parietals is impossible to calculate because the contact between parietal and intertemporal is not visible. If we consider the width of parietal + intertemporal relative to parietal length, the ratio is 0.43; the ratio for the parietal alone, then, is equal to or less than this value. Even this maximum value highlights the slender snout expected of a *Eusthenopteron* species (0.38 in *E. foordi*; Jarvik, 1944a). The ratio is 0.5 or greater in those tristichopterids with wide skulls with blunt snouts. These include *C. burnsi* (AM F96856; Ahlberg and Johanson, 1997), *E. wängsjöi* (MNHN.F.ARD 242; Clement, 2002), and *H. lindae* (ANSP 20935A, 22359; Daeschler and Downs, 2018).

The premaxilla of *E. jenkinsi* has several enlarged teeth (pmx, Fig. 3B') at the mesial end of the tooth row but no defined tusk (premaxilla morphotype B of Borgen and Nakrem, 2016). This is similar to the condition in *E. foordi* (Jarvik, 1944a), *E. obruchevi* (Vorobyeva, 1977), and *E. säve-*

söderberghi (Jarvik, 1942). This character is unknown in the other *Eusthenopteron* species. The premaxilla of *E. jenkinsi* does not exhibit the caudal symphyseal process that reaches to the vomer to divide the apical fossa in *Heddeleithys dalglesiensis* (Snitting, 2009) and appears to do so in *H. lindae* (Daeschler and Downs, 2018).

Postparietal Shield. The one known postparietal shield for *E. jenkinsi* (NUFV 1187; Fig. 2C) is associated with the otic-occipital and therefore may not be assessed in visceral view. In dorsal view, none of the contacts are visible among the postparietal, supratemporal, and tabular elements. The postparietal shield is short and broad for a species of *Eusthenopteron* and exhibits a width-to-length ratio (1.75) that is more comparable to those of derived tristichopterids with wide heads: *E. wängsjöi* (1.75; Johanson and Ahlberg, 1997) and *H. lindae* (1.67 in ANSP 23867; Daeschler and Downs, 2018). A long, depressed, unornamented zone of overlap for the extrascapular series extends along the caudal margins of postparietal and tabular (Fig. 2C). It does not extend to the medial corner of the postparietal nor the lateral corner of the tabular. A short unornamented zone of overlap for parietal and intertemporal extends along the rostral margin of postparietal and supratemporal. Only a shallow concavity along the lateral margin of the postparietal shield suggests the presence of a spiracular opening in the skull roof.

Cheek. The only identifiable cheek element in *E. jenkinsi* is a single isolated maxilla (NUFV 1199; Fig. 2D). The maxilla is a long, narrow element with its greatest height between its contacts with squamosal and jugal. This matches the condition in *E. foordi* (Jarvik, 1944a), *Tristichopterus alatus* (Traquair, 1875), *H. dalglesiensis* (Snitting, 2009), *Platycephalichthys bischoffi* (Vorobyeva, 1962), *H. lindae* (Daeschler and Downs, 2018) and *E. cf. wängsjöi* (AMF122164;

Johanson, 2004). The maxilla of *E. jenkinsi* carries long, depressed zones of overlap along its dorsal margin to accommodate the lacrimal and jugal rostrally and the squamosal caudally. Among tristichopterids, a maxilla overlapped by all three of these cheek elements is additionally reported in *E. wängsjöi* (Jarvik, 1985), *E. cf. wängsjöi* (AMF52689; Johanson, 2004), and *P. bischoffi* (Vorobyeva, 1962). The rostral end of the lacrimal overlap zone extends dorsally to form a process that appears to form the lateral border of the choana. This process is also described in *E. foordi* (Jarvik, 1944a), *E. wängsjöi* (Jarvik, 1952, 1985; Johanson and Ritchie, 2000), *E. cf. wängsjöi* (AMF122164; Johanson, 2004), and *Edenopteron keithcrooki* (Young et al., 2013).

Ethmosphenoid and Dermal Palatal Elements. The ethmosphenoid of *E. jenkinsi*, including the nasal capsules and dermal bones of its palatal surface, is known in detail from three complete specimens (NUFV 1187, 1201 [Fig. 3A], and 1245 [Fig. 3B]). The ethmosphenoid carries three separated sites of contact with the otic-occipital; the first is dorsal to the cranial cavity and the remaining pair wrap around the caudal and lateral surfaces of the two processus connectens (p.con, Fig. 3A'). The length ratio of ethmosphenoid to otic-occipital is as described above for parietal and postparietal shields. The ethmosphenoid is long and narrow in *E. jenkinsi*. The ratio of width (across the nasal capsules) to length in the least distorted specimen (NUFV 1245) is 0.28. This is narrower than Jarvik's (1954) reconstruction of the *E. foordi* ethmosphenoid (~0.40), based on his grinding series of P.222.

The basipterygoid process (b.p, Fig. 3A') is a prominent feature of the lateral ethmosphenoid. It is a deep, crescent-shaped contact surface for the basal articulation of the palatoquadrate, more pronounced and com-

plex here than it is in *E. foordi* (Jarvik, 1954). The process comprises a short vertical back wall and a long ventral platform that dips ventrally at its rostral end. Dorsal and just rostral to the basipterygoid process is the suprapterygoid process (s.p, Fig. 3A'). It appears as a ventral ledge with a depression just dorsal to it; it serves as the contact surface for the processus ascendens of the palatoquadrate.

The foramen for cranial nerve III (n.III, Fig. 3A') appears just rostral to the dorsal terminus of the basipterygoid process, and the larger foramen for nerve II (n.II, Fig. 3A'), set within a fossa, is rostral to this. A knoblike process ventral to the nerve II foramen appears to have a contact site (c.s, Fig. 3A') on its ventral surface and may represent an additional site of contact between ethmosphenoid and palatoquadrate. A wide longitudinal groove (gr, Fig. 3A') bordered by dorsal and ventral crests extends rostrally and slopes dorsally from the position of nerve II. This same groove in *E. foordi*, identified by Jarvik (1954) as the origin of the levator bulbi muscle, slopes ventrally rather than dorsally. The postnasal wall is penetrated by a large circular foramen (the fenestra endonarina posterior of Jarvik, 1954; f.en.p, Fig. 3B').

At the caudal end of the ethmosphenoid, the concave, rugose notochord pit (not.p, Fig. 3B') is bordered dorsally by the two processus connectens. These processes are separated by a deep notch that bisects the short roof of the ethmosphenoid's notochordal chamber. The cranial cavity dorsal to the processus connectens is bordered laterally by the rounded caudal edges of the ethmosphenoid's lateral walls.

The parasphenoid (psph, Fig. 3B') of *E. jenkinsi* is a narrow element that appears to terminate at about the level of the caudal vomerine fang's caudal margin. Rostrally to the parasphenoid, the vomers (vo, Fig. 3B')

are in contact with one another but for a short intervomerine canal (iv.c, Fig. 3B'). The denticulated plate (d.psph, Figs. 3A', B') is a raised, ventral keel that narrows to a rostral point that reaches nearly to the rostral end of the parasphenoid. A narrow, raised denticulated plate appears in tristichopterids, except for presumed derived forms like *H. lindae* (Daeschler and Downs, 2018), *E. wängsjöi* (Jarvik, 1954), and *M. fairfaxi* (Johanson et al., 2003). The denticulated surface of the parasphenoid is penetrated at its caudal end by the buccohypophysial foramen (bh.f, Fig. 3B').

The vomer exhibits a fang pair (v.f, Fig. 3A') and a tall vertical lamina that wraps around its labial edge. The vertical lamina is nearly as tall as the fangs that it surrounds and is crowned by a continuous row of marginal teeth that are on a smaller size scale than those of the premaxilla just labial to it. In the three known palatal specimens of *E. jenkinsi* (NUFV 1187, 1201, 1245), left and right vertical laminae do not contact one another across the midline. The vomerine fangs are circular in cross section, but with a distinct mesial and distal cutting edge. The rostromedial vomer shares a contact with the premaxilla, the caudal limit of which is the mesial border of the choana. The apical fossa is divided along the midline by a ventral ridge of the ethmoid. The vomer does not exhibit a rostral-directed process to contact a caudal-directed one of the premaxilla. Such a dermal division of the apical fossa is only known in *H. dalglesiensis* (Snitting, 2009), although its presence in *H. lindae* is inferred (Daeschler and Downs, 2018).

Unusual for a primitive tristichopterid, the caudolateral margin of the *E. jenkinsi* vomer is interrupted by a distinct corner. This corner represents the caudal margin of the vomer's dorsal contact with the entopterygoid; it is not present in the other described species of *Eusthenopteron* for which the

element is known (*E. foordi*, Jarvik, 1944a; *E. säve-söderberghi*, Jarvik, 1937). In these species, the caudolateral vomerine margin is smooth and concave. In *E. jenkinsi*, the margin extends along the long caudal vomerine process that is typical for a tristichopterid. The process makes for a long contact with the parasphenoid. The vomer-parasphenoid contact is one third the length of the entire parasphenoid, although an exact measurement is only possible in one specimen (0.33, NUFV 1245).

Otic-Occipital. After *E. foordi*, NUFV 1187 (Fig. 4) represents the best known otic-occipital for a species of *Eusthenopteron*. The extent of ossification in the *E. jenkinsi* otic-occipital is more similar to the condition in *M. fairfaxi* than to that in *E. foordi* (Johanson et al., 2003). In *E. jenkinsi*, as in *M. fairfaxi*, the basicranium is unossified such that the notochordal tunnel is exposed ventrally. Additionally, both species show ossification in the otic shelves, lateral commissures, and exoccipitals. The exoccipitals differ from those of *M. fairfaxi* in that they form only the dorsal and lateral margin of the foramen magnum. NUFV 1187 shows no ossified ventral margin of the foramen magnum, and the exoccipitals do not exhibit any ventral extensions like those that contribute to the notochordal canal in *M. fairfaxi* (Johanson et al., 2003). Unfinished surfaces of the exoccipital appear dorsal and lateral to the foramen magnum. The lateral unfinished surfaces appear similar to those in *M. fairfaxi* that Johanson et al. (2003) interpret to be vertebral articulations supporting a mobile neck joint.

The lateral commissure carries dorsal and ventral teardrop-shaped articulation sites for the hyomandibula (h.art, Fig. 4A'). Both face caudally, although the dorsal articulation appears to exhibit a slight dorsal inclination. The ventral articulation for the hyomandibula lies directly beneath the dor-

sal articulation rather than rostral to it, as in *E. foordi* (Jarvik, 1980), or caudal to it, as in *M. fairfaxi* (Johanson et al., 2003). The vertical stacking of these articulation sites supports a horizontal orientation of the proximal hyomandibula; this is unlike the oblique orientation in *E. foordi* (30° ventral from the frontal plane according to Smithson and Thomson, 1982).

The jugular canal (j.c, Fig. 4A') passes rostrally through the lateral commissure just dorsal to the ventral attachment site for the hyomandibula. The canal continues as a groove (j.gr, Fig. 4A') along the lateral otic-occipital and dorsal surface of the otic shelf. No bridge of bone stretches across the canal after it exits the lateral commissure, as was reconstructed in *E. foordi* by Jarvik (1954). Two tiny foramina penetrate the lateral surface of the otic shelf in the position of the canals for the orbital artery and the palatine ramus of nerve VII (as identified in *E. foordi* by Jarvik, 1954). A larger foramen appears on the lateral face of the otic-occipital just dorsal to the caudal end of the otic shelf. A foramen in the same position was identified as the spiracular canal in *E. foordi*, although this is but the largest of several foramina described in this same area (Jarvik, 1954). The position of the foramen for nerve V is impossible to discern in NUFV 1187.

The basicranial fenestra (bas.f, Fig. 4B') is incomplete caudally as a result of the limited ossification. The ventral margin of the cranial cavity's lateral walls, in the position of the basicranial fenestra, is lacking perichondral bone. This lends support to the possible presence of a ventral arcual plate, although one has not yet been recovered for the species. Each otic shelf (ot.s, Fig. 4B') projects rostrally and narrows to a blunt process (av.p; Fig. 4B') with a contact site for the processus connectens on its medial surface. A shallow crest (ot.cr; Fig. 4B')

extends along the ventrolateral otic shelf and deepens into a vertical bladeliike process at the shelf's caudal end; no such process is seen in *E. foordi* (Jarvik, 1954). The internal wall of the otic shelf has a wide longitudinal groove to accommodate the dorsal notochord. The ventral surface of the single otic-occipital specimen (NUFV 1187) only preserves the lateral margins of the basicranial fenestra and the rostral and lateral margins of the fenestra ovalis. These openings are continuous with the large depression that takes the place of the basicranium and ventrally exposes the internal otic capsules (ot.c, Fig. 4B') and cranial cavity. The missing basicranium is outlined by unfinished bone that is symmetrical across the midline. This preservation supports an interpretation of a lack of basicranial mineralization in life rather than weathering or other damage to the skull after death.

At the caudal end of the otic-occipital, only dorsal features are preserved because of the low level of ossification. These include the crista parotica and all the bone surrounding the fossa bridgei, exoccipitals, and the braincase dorsal to the cranial cavity. On the caudal surface of the otic-occipital, dorsal and just lateral to the cranial cavity, there is a foramen identified in *E. foordi* as the canal for the occipital artery by Jarvik (1954).

Hyomandibula. The preserved portion of the *E. jenkinsi* hyomandibula (NUFV 1057, 1186 [Fig. 5]) matches the general description for that of *E. foordi*. It is boomerang-shaped with a hyomandibular canal (hy.c, Fig. 5A) passing through the element at midlength and continuing as grooves on the medial surface at the proximal end and the lateral surface at the distal end. The hyomandibula of *E. jenkinsi* exhibits a bicipital contact surface (Fig. 5B) with the lateral commissure of the otic-occipital. Each contact is convex and piriform in outline, with the narrow ends

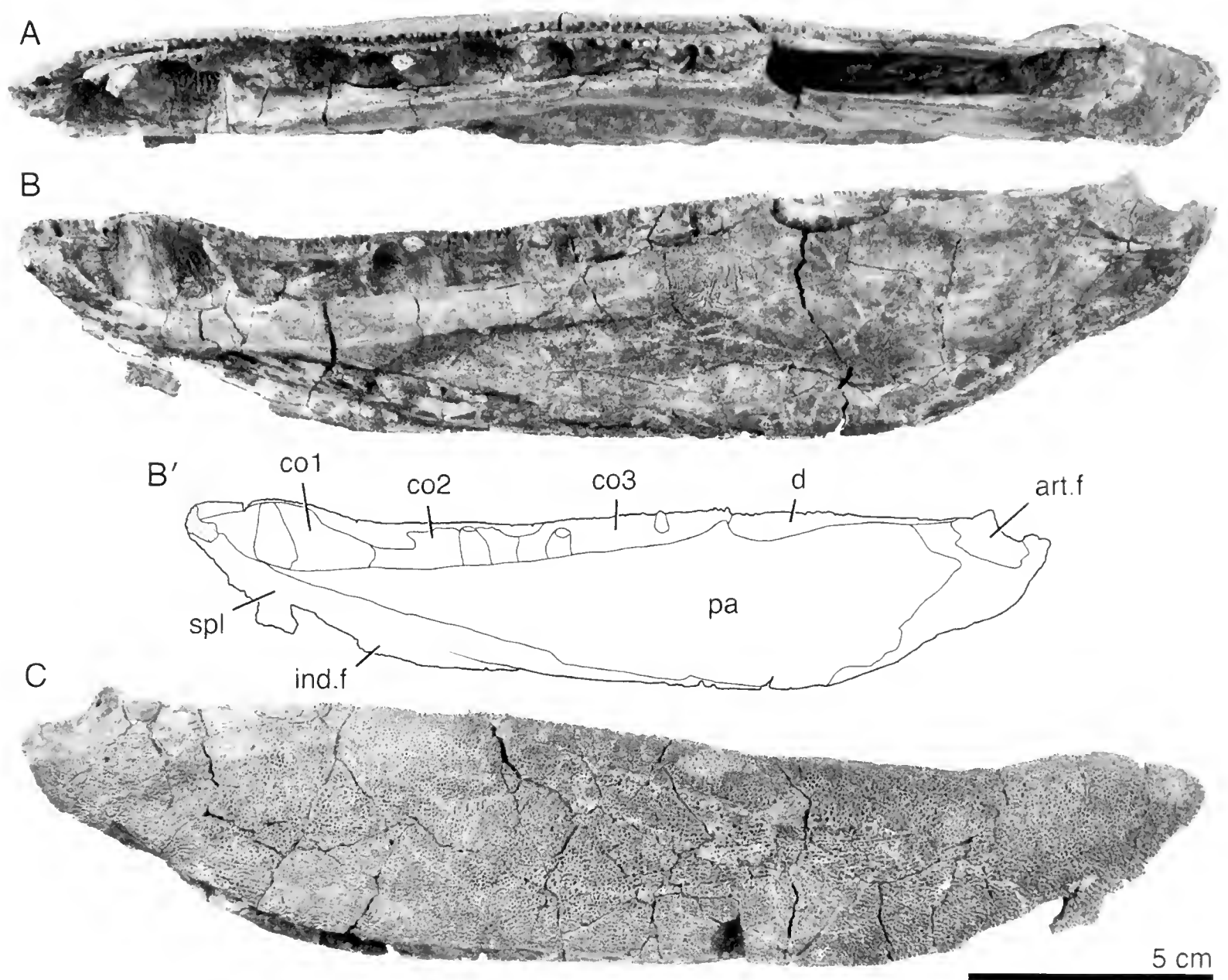


Figure 6. *Eusthenopteron jenkinsi* sp. nov., NUFV 1178, right lower jaw in (A) coronal, (B) lingual (B', labeled illustration), and (C) labial views. Abbreviations: art.f, articular facet for the quadrate; co1, coronoid 1; co2, coronoid 2; co3, coronoid 3; d, dentary; ind.f, infradental flange; pa, prearticular; spl, splenial.

pointing toward one another. The hyomandibula is thickest at midlength, and this thickened portion (the preopercular process of Smithson and Thomson, 1982; pop.pr, Fig. 5C) carries a longitudinal, elongated rugosity at middepth. The rugosity is inferred to be the contact site for the cheek skeleton. *Eusthenopteron foordi* has a seemingly different rugosity along the hyomandibula's dorsolateral edge that Jarvik (1954) interprets to be a contact site for the opercular; however, Smithson and Thomson (1982) and Westoll (1943) note the lack of any visible opercular contact surface in the

E. foordi material available to them. The two hyomandibula specimens of *E. jenkinsi* lack the dorsal margin, so the presence of such a contact site is unknown. Dorsal to the preopercular process, the hyomandibula is observed to be depressed; this depression may represent the insertion of the protractor hyomandibularis, as proposed for *E. foordi* by Smithson and Thomson (1982).

Lower Jaw. In *E. jenkinsi*, the fangs of coronoid 1 are especially large, and the remaining fang pairs decrease in size, mesial to distal (Fig. 6). There are two fang pairs on the third coronoid. The presence of more

than one fang pair on the third coronoid is unique to tristichopterids (Ahlberg and Johanson, 1998; Snitting, 2008; Porro et al., 2015) and is present in most species with a few known exceptions: *Spodichthys buetleri* (Snitting, 2008) and the species of *Tristichopterus* (Snitting, 2008; Zupinš, 2008; Bishop, 2013). In *E. jenkinsi*, coronoid 3 is significantly longer than the first two. This is considered by Borgen and Nakrem (2016:448) to be a “necessary character” in *Eusthenopteron*, but it is also present in all other tristichopterid species with more than one coronoid 3 fang pair (Ahlberg and Johanson, 1998; Snitting, 2008).

Cutting edges are present on some but not all of the coronoid fangs of *E. jenkinsi*. Jarvik (1937) found variation in coronoid fang cross sections in *E. foordi*, even within a single specimen, and so concluded that this feature was of no diagnostic value. All three coronoids of *E. jenkinsi* bear a vertical lamina with a marginal tooth row. This condition is also present in *E. foordi* (Jarvik, 1944a), *E. wenjukowi* (Vorobyeva, 1977), *Notorhizodon mackelveyi* (Young et al., 1992), and *Tinirau clackae* (Swartz, 2012). Marginal teeth are restricted to the third coronoid in *C. burnsi* (Ahlberg and Johanson, 1997), *E. wängsjöi* (Johanson and Ahlberg, 1997), and *M. fairfaxi* (Johanson and Ahlberg, 1997). *Heddeleithys dalglei-siensis* (Snitting, 2009) and *P. bischoffi* (Vorobyeva, 1962) show marginal teeth on both second and third coronoids. In *E. jenkinsi*, the marginal coronoid tooth row continues labially around the fangs but is interrupted in the positions of both intercoronoid fossae (Fig. 6A). The interruption between coronoid fangs 1 and 2 occurs in all specimens of *E. foordi*, but between coronoid fangs 2 and 3, the condition is variable (Borgen and Nakrem, 2016). Like the condition in *E. foordi* (Borgen and Nakrem, 2016), the marginal coronoid tooth row is

continuous between the two fang pairs of coronoid three. Best viewed in NUFV 1178 (Fig. 6A), the two coronoid fang pairs of coronoid 3 themselves are part of a continuous second row of larger teeth that is lingual to the marginal row and extends along the entire length of the element except for the most mesial end (Fig. 6A).

The dentary tooth row extends to the symphysis; the most mesial four or five dentary teeth are successively larger in size but there is no dentary fang. Borgen and Nakrem (2016:448) cite this condition (their dentary dental morphotype B) as potentially diagnostic for the grouping *Eusthenopteron*. Dentary fangs appear in all but a group of tristichopterid species that are presumed to be primitive: the species of *Eusthenopteron* (Jarvik, 1980), *Spodichthys* (Snitting, 2008), and *Tristichopterus* (Snitting, 2008). An unassigned tristichopterid mandible from Scotland is also without dentary fangs (Parfitt et al., 2014). In *E. jenkinsi*, the mesial end of the dentary widens to form a lingual shelf that forms the symphyseal pit and the mesial margin of the precoronoid fossa. A raised rugosity formed of this dentary shelf and the splenial likely accommodated a parasymphysial tooth plate (adsymphysial of Porro et al., 2015), although none is associated with the material.

The infradental flange (ind.f, Fig. 6B') is formed by the splenial (infradentary 1), as is the thick lingual margin of the precoronoid fossa and, together with the dentary, the mandibular symphysis. There is no visual support for a postsymphysial element, as is proposed for *E. foordi* from computed tomography (CT) images (Porro et al., 2015). The postsymphysial of *E. foordi* is interpreted to be a novel dermal ossification that separates the splenial from the precoronoid fossa, the mandibular symphysis, and the attachment site for the parasymphysial tooth plate (Porro et al., 2015). The ventral

margin of the jaw in *E. jenkinsi* is entirely formed by the unornamented part of the four infradentaries; these wrap under the jaw to contact the prearticular along the ventro-lingual edge. There does not appear to be any Meckelian exposure along the jaw's ventral margin; the Porro et al. (2015) interpretation of *E. foordi* CT data includes small gaps in the infradentaries that expose Meckelian ossification. The dorsodistal corner of the infradentary 4 (surangular) labial surface (Fig. 6C) is unornamented and forms an overlap surface for the cheek.

Pectoral Girdle. The scapulocoracoid (Fig. 7A) of *E. jenkinsi* is similar to that of *E. foordi* (Andrews and Westoll, 1970). The glenoid surface (gl, Fig. 7A') is concave and pear-shaped (wide portion medial), and a groove separates it from the visceral surface of the caudal cleithrum. A medial ridge runs from the dorsomedial corner of the glenoid to the subscapular fossa. The glenoid foramen pierces this ridge close to the glenoid. The scapulocoracoid has a tripodal support against the cleithrum; supraglenoid (sgl.b, Fig. 7A') and infraglenoid buttresses (igl.b, Fig. 7A') provide craniodorsal and cranio-ventral support to the glenoid, which itself forms the third leg of the tripod. Pairs of these buttresses border gaps in the scapulocoracoid that communicate with the space enclosed by the tripodal structure: subscapular fossa between supraglenoid and infraglenoid buttresses and supraglenoid foramen between glenoid and supraglenoid buttress. Deformation of NUFV 1203 may explain the lack of a supracoracoid foramen (as observed in *E. foordi*) between the glenoid and infraglenoid buttress, but the massive nature of its infraglenoid buttress suggests that the foramen would have been quite narrow if one was present. The size of the infraglenoid buttress in NUFV 1203 is such that it extends cranially beyond the edge of the

cleithrum to make direct contact with the clavicle.

Although cleithrum shape varies widely within *E. foordi* (Borgen and Nakrem, 2016), *E. jenkinsi* is broadly consistent with the condition observed in that species. The caudal margin has a bent outline with a projecting heel that contrasts with the continuously curved margin observed in *E. farloviensis* (White, 1961). A short pointed cranial process overlaps the clavicle just dorsal to a broad zone of overlap of clavicle onto cleithrum. This overlap zone extends along a long ventral process (v.p, Fig. 7A') of the cleithrum that is more similar to the one in *E. foordi* than to the short, underdeveloped process of *E. farloviensis* (Jarvik, 1944b; White, 1961). The deep, coarse ornament of the *E. jenkinsi* cleithrum comprises pits and short grooves separated by sharp ridges. The ornament is finely pitted along the ventral process and along the cranial and caudal margins of the dorsal lamina. Unlike the condition in most specimens of *E. foordi*, the cranial edge of NUFV 1203 does not exhibit a broad unornamented overlap zone for the opercular series (Andrews and Westoll, 1970). Only a short, depressed, unornamented flange appears along the cleithrum's cranial margin in the bend between its dorsal and ventral (scapulocoracoid-bearing) laminae.

A second specimen of cleithrum and scapulocoracoid, NUFV 1198 (Figs. 7D–G), belongs to a different size category than NUFV 1203. We do not refer NUFV 1198 to *E. jenkinsi* here, but if it did belong to this species, the anatomical differences between NUFV 1198 and 1203 might be explained by different ontogenetic stages. In describing NUFV 1198, we focus on the anatomy that is different from the condition in NUFV 1203. The glenoid and buttresses that compose the scapulocoracoid of NUFV 1198 are slender and widely spaced, enclosing large

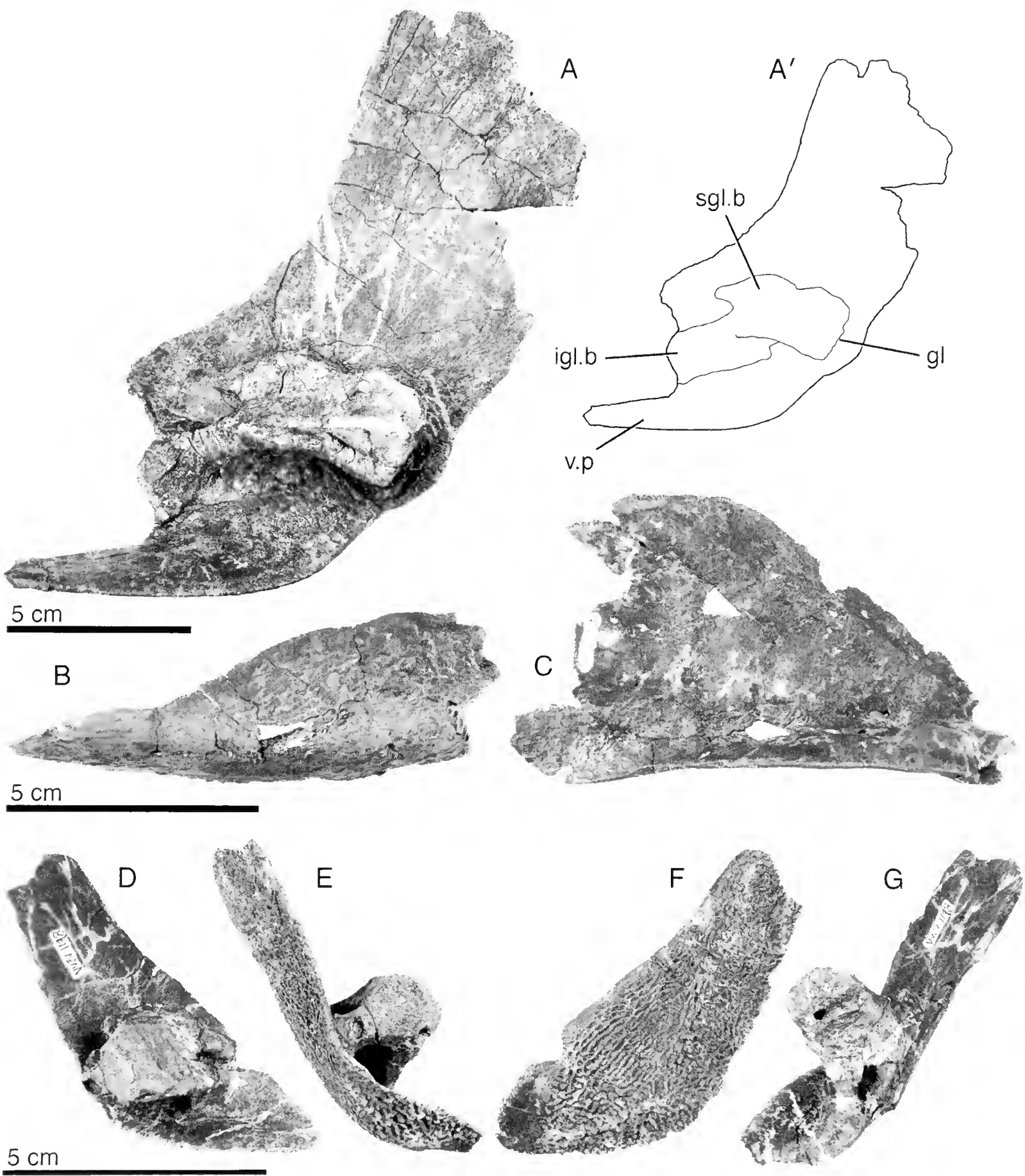


Figure 7. A–C, *Eusthenopteron jenkinsi* sp. nov. A, NUFV 1203, right cleithrum and associated scapulocoracoid in visceral view (A', labeled illustration); B–C, NUFV 1206, left clavicle in (B) lateral and (C) dorsal views; D–G, Tristichopteridae indet., NUFV 1198, left cleithrum and associated scapulocoracoid in (D) visceral, (E) caudal, (F) lateral, and (G) cranial views. Middle scale bar applies to B–C; lower scale bar applies to D–G. Abbreviations: gl, glenoid; igl.b, infraglenoid buttress; sgl.b, supraglenoid buttress; v.p, ventral process of the cleithrum.

open subscapular fossa and supraglenoid and supracoracoid foramina. The glenoid itself is concave and pear-shaped with the narrow, lateral portion more deeply recessed and pitlike than the wide, medial portion. The cleithrum has no distinct bend between dorsal and lateral lamina, giving the element a broadly curved appearance more similar to the one observed in *E. farloviensis* (White, 1961). Its cranial process above the zone of clavicle underlap is rounded and very short. The ornament of NUFV 1198 is similar to that of the larger specimen but accordingly more fine than the coarse features there. The cranial margin of the cleithrum is unornamented and does not exhibit a depressed zone in the cranial bend.

The clavicle of *E. jenkinsi* is represented by two specimens (NUFV 1197, 1206 [Figs. 7B, C]); both are incomplete at cranial and caudal ends and do not preserve the area of overlap onto the interclavicle nor the ascending process that is overlapped by the cleithrum. In other regards (shape, ornament, overlap zone onto cleithrum), the clavicle of *E. jenkinsi* matches the condition described for *E. foordi* (Jarvik, 1944b; Andrews and Westoll, 1970).

Fin Bones. The humerus of *E. jenkinsi* (Figs. 8A–D) is a broad, dorsal-ventrally flattened block that narrows from the glenoid articulation to the radial-ulnar facets. The glenoid articulation (gl.a, Fig. 8C) is oval (long axis is preaxial–postaxial), not pear-shaped (preaxial end narrow) as it is in *E. foordi* (Andrews and Westoll, 1970). It is concave, deeply rugose, and restricted to the proximal surface of the bone. Ulnar (u.f, Fig. 8D) and radial (r.f, Fig. 8D) articulations are convex; the ulnar articulation is nearly parallel to that of the glenoid, and the radial articulation is obliquely oriented toward the preaxial direction. On the dorsal surface of the humerus, the supinator, deltoid, and ectepicondyle (ect, Fig. 8B) fuse together to

form a robust tuberosity that narrows distally and does not appear to be penetrated by supinator nor ectepicondyle foramina in the two known specimens (NUFV 1187, 1200). The ectepicondyle of *E. jenkinsi* is so distal in position that it reaches the distal margin of the humerus. This is similar to the condition in the presumed derived tristichopterids *C. burnsi* (Ahlberg and Johanson, 1997), *H. lindae* (Daeschler and Downs, 2018), and *M. fairfaxi* (Johanson and Ahlberg, 1997) and unlike that of *E. foordi*, where the feature appears at midlength along the humerus (Andrews and Westoll, 1970). In *E. jenkinsi*, and in *H. lindae*, the ulnar facet does not extend onto the ectepicondyle as it does in *C. burnsi* (Ahlberg and Johanson, 1997; Daeschler and Downs, 2018).

As is typical for a tristichopterid humerus, the entepicondyle is joined to an oblique, fluted ridge (ent.r, Fig. 8A) that extends across the ventral surface of the bone. The ridge is penetrated by small foramina along its length and a larger entepicondyle foramen (ent.f, Fig. 8C, D) at the postaxial margin of the ulnar facet. As in most specimens of *E. foordi*, the ventral edge of the ridge is unfinished bone and may have been cartilaginous in at least the two individuals represented by the material (Andrews and Westoll, 1970). The ventral ridge shallows proximally and terminates at the glenoid attachment. It does not exhibit a proximal knoblike process interpreted, in *E. foordi*, to be the insertion site for the pectoralis muscle (Andrews and Westoll, 1970).

The ulna (Fig. 8E) is a short, blocky element that increases in width at both proximal and distal ends. The distal end is wider than the proximal and accommodates two convex sites of articulation for distal mesomeres. Relative to the postaxial articulation, the preaxial one is smaller, deeply set, and obliquely angled. The humeral facet on

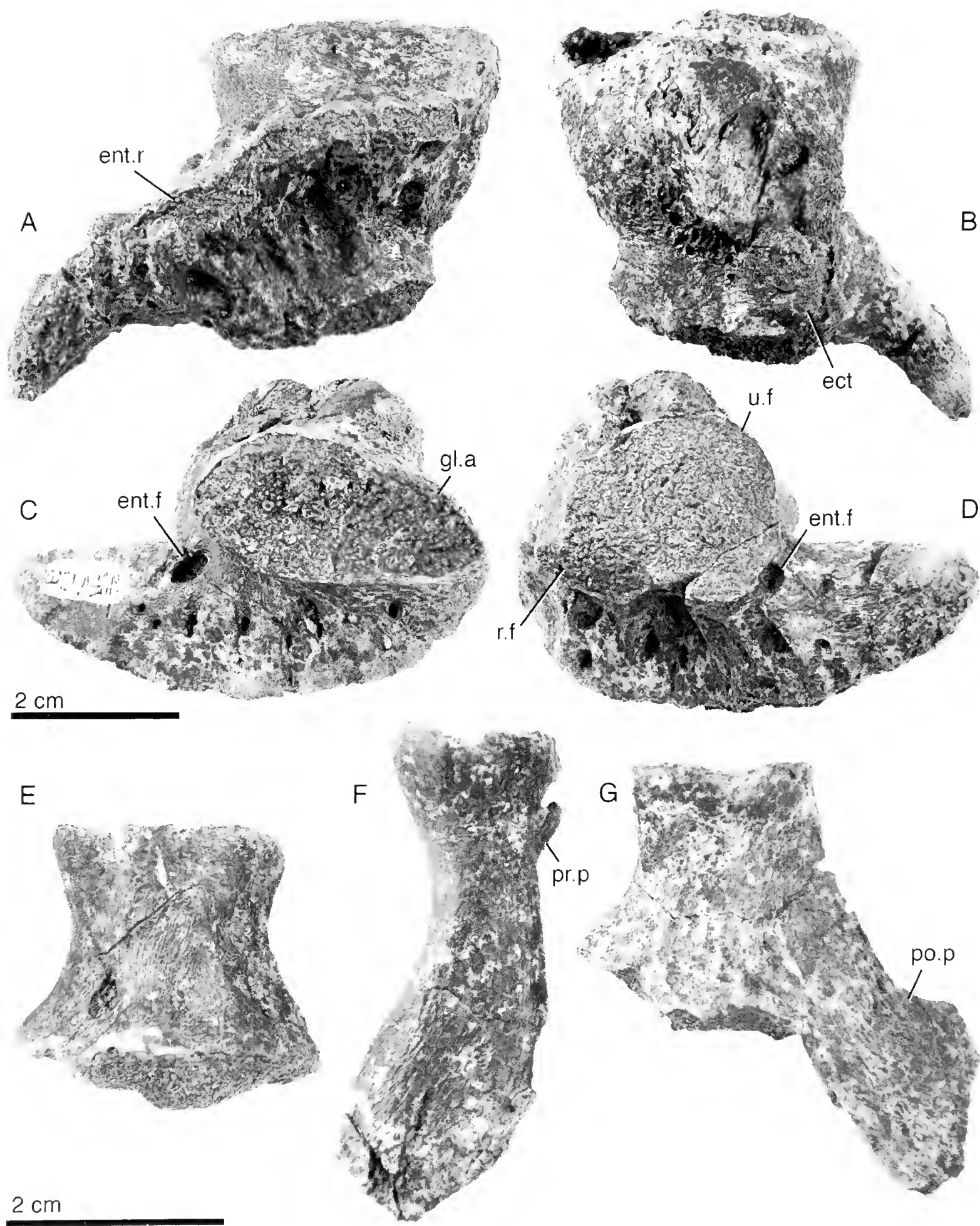


Figure 8. *Eusthenopteron jenkinsi* sp. nov., A–D, NUFV 1200, left humerus in (A) ventral, (B) dorsal, (C) proximal, and (D) distal views; E, NUFV 1180, left ulna in dorsal view; F, NUFV 1184, right radius in dorsal view; G, NUFV 1179, unidentified fin mesomere in dorsal or ventral view. Upper scale bar applies to A–D; lower scale bar applies to E–G. Abbreviations: ect, ectepicondyle; ent.f, entepicondyle foramen; ent.r, entepicondyle ridge; gla, glenoid articulation; po.p, postaxial process; pr.p, preaxial process; r.f, radial facet; u.f, ulnar facet.

the proximal ulna is oval-shaped (preaxial-postaxial long axis) and flat to slightly concave with a round dimple in the center. Similar to the condition in *E. foordi* (Andrews and Westoll, 1970), a wide longitudinal ridge with a pair of sharp crests extends along the ulna in a postaxial, ventral position. Unlike *E. foordi*, however, the ridge terminates distally in a short extension of the ulnare articulation onto the ulna's ventral surface. Andrews and Westoll (1970) describe four crests in *E. foordi*, one each to separate dorsal and ventral surfaces from preaxial and postaxial surfaces; *E. jenkinsi* exhibits only the two postaxial crests.

The radius (Fig. 8F) has a circular, concave humeral articulation facet. Distally from the humeral facet, the radius narrows dramatically to a thin cylinder that is then dorsal-ventrally flattened and broadened into a blade with a rounded distal margin. As in *E. foordi*, just distal to the humeral articulation, preaxial and ventral in position, a flat process (pr.p., Fig. 8F) reaches proximally from the radius. In a position just dorsal to the process, the humeral articulation exhibits a short extension onto the shaft of the radius. This too is consistent with the condition in *E. foordi* (Andrews and Westoll, 1970).

One fin mesomere specimen (NUFV 1179; Fig. 8G) is anatomically consistent with both ulnare and fibula, so a definitive identification is impossible. It is very similar to the ulna in shape, including its articulations at proximal and distal ends, excepting one feature. A long, dorsal-ventrally flattened postaxial process (po.p., Fig. 8G) extends from the postaxial-distal corner of this mesomere. The process nearly doubles the length of the element.

DISCUSSION

Jarvik (e.g., 1942, 1944a, 1944b, 1954, 1980, 1996) described the cranial and post-

cranial anatomy of *E. foordi* in exhaustive detail in a series of monographic treatments. The author used the skeletal descriptions as the basis for considerable inferences into the soft tissue anatomy and physiology of the species. Despite this anatomical understanding, the taxonomic diagnosis of the species and of the grouping *Eusthenopteron* has received far less attention through the years. Here we provide a review of the taxonomic history of *Eusthenopteron*. The clarity gained from this review is a necessary condition before we may support our above diagnosis for *Eusthenopteron*.

Jarvik's descriptive work was made possible by the remarkable collection of many well-preserved *E. foordi* specimens from the type locality, Miguasha (Escuminac Formation, Frasnian) on the southern shore of Gaspé Peninsula, Quebec, Canada. A. H. Foord collected the *E. foordi* type material from this location ("north bank of the mouth of Restigouche River," Whiteaves, 1881:494) in 1880. Whiteaves (1881) named the grouping and species and noted a particular affinity with *T. alatus* (Egerton, 1861); this is the original recognition of the eventual grouping Tristichopteridae named by Cope (1889). Whiteaves (1881) based the affinity on the presence of three pterygiophores ("fin rays," Whiteaves, 1881:495) in the second dorsal and anal fins. The names "*Tristichopterus*" and "Tristichopteridae" make direct reference to this trio of rodlike structures in the fin.

The original Whiteaves (1881) diagnosis for *Eusthenopteron* lists three features that are meant to distinguish the new grouping from *Tristichopterus*. The first, "vertebral centers are not ossified" (Whiteaves, 1881:495), was discounted by the subsequent discovery of ossified inter- and pleurocentra in *E. foordi* (Traquair, 1890; Jarvik, 1952; Andrews and Westoll, 1970). The second, "caudal [fin] ossicles are articulated to

modified haemal spines" (Whiteaves, 1881:495), appears in even the type material of *T. alatus* and is well illustrated in Egerton (1861, pl. IV, fig. 2). This second feature was the product of Whiteaves's (1881) mistaken understanding that the caudal fin "osselets" (Whiteaves, 1881:495) of *E. foordi* and the "interspinous bones" (Egerton, 1861:51) of *T. alatus* are two different things. Eight years later, Whiteaves (1889:89) corrects this mistake by noting that the ventral caudal fin supports of *E. foordi* and *T. alatus* "are not essentially different in their nature." Whiteaves's (1881) third and final point of contrast between *Eusthenopteron* and *Tristichopterus* is the size (larger in *Eusthenopteron*) and shape (unspecified) of the pterygiophores of the second dorsal and anal fins. This noted difference was presumably affected by the lack of collected material from both groupings at the time of publication. Whiteaves (1881) also provides a short alpha-level diagnosis for *E. foordi*. He cites only a large body size ("two feet or more") and a "narrowly elongated and acutely pointed first dorsal fin" (Whiteaves, 1881:495). We suspect that these are simply the fourth and fifth features meant only to contrast the taxon with *T. alatus*, considering both *Eusthenopteron* and *Tristichopterus* were monospecific at the time of publication.

Two years later, Whiteaves (1883) expanded the diagnoses of *Eusthenopteron* and *E. foordi* but did not drop any of the features cited in his 1881 publications. Although no new *Eusthenopteron* species were described in the ensuing years, all five diagnostic features of Whiteaves (1881) were slightly revised to become the *E. foordi* specific diagnosis in the 1883 publication. The new diagnosis of the *Eusthenopteron* grouping was a long list of newly realized, mostly postcranial features. This list is too lengthy to reproduce here but among the many new postcranial features, all but two are qualitative shape character-

istics. Of those remaining two, neither is presently diagnostic of *Eusthenopteron*: the presence of two dorsal fins and ossified neural spines, haemal spines, and "interspinous bones" (Whiteaves, 1883:30). There are only two cranial features listed in Whiteaves's (1883) *Eusthenopteron* diagnosis, neither of which is currently unique to *Eusthenopteron* or to *E. foordi*. The first is "densely and irregularly corrugated" or "tubercular" ornament and the second is "compressed-conical" teeth with a sharp cutting edge (Whiteaves, 1883:30).

In his 1889 publication, Whiteaves questions whether *E. foordi* should have been described as a species of *Tristichopterus* and reduces the list of distinguishing characteristics. He cites only four features meant to differentiate *Eusthenopteron* from *Tristichopterus* but states that he is unsure whether the differences are "of generic or of only specific importance" (Whiteaves, 1889: 90). Among the four features in *Eusthenopteron*, only one, at least in how it is articulated, appears for the first time in this publication. This is a true interspinous (between vertebral spinous process and radials) basal pterygiophore in the second dorsal and anal fins. Egerton (1861:52) refers to the same element in *Tristichopterus* as a "spinous" bone and suggests it may have formed from the fusion of spinous processes. This distinction between spinous and interspinous origins is dismissed by Traquair (1890), who considers the pterygiophores in both groupings to be interspinous. In his diagnosis of *Eusthenopteron*, Traquair (1890) retains only two of Whiteaves's (1889) four features: a dorsal-ventrally symmetrical caudal fin and cutting edges on the fangs. Both of these are then explicitly dismissed by Jarvik (1937).

Jarvik (1937) cites two differences that he notices between *Eusthenopteron* and *Tristichopterus*. The first is a very slight difference in the relative depth of the caudal fin dorsal

to the body axis (one third the total height in *Eusthenopteron* and three sevenths in *Tristichopterus*). The second is a slight difference in the length ratio of parietal shield to total skull length (0.65 in *Eusthenopteron*, 0.58 in *Tristichopterus*). Jarvik (1937:70) admits that a new diagnosis is needed for *Eusthenopteron* and writes of his intention to provide one in a future monograph. Although he would continue to write on the topic of *Eusthenopteron* for another 60 years, Jarvik never did return to the question of the taxon's diagnosis (Cloutier, 1996).

Cloutier (1996) reviews the taxonomic work of Vorobyeva and Obruehev (1964) and Long (1985) and provides a diagnosis of *Eusthenopteron* that is based entirely on cranial dimensions and fin positions. The relevant cranial dimensions are the length ratios of orbit to parietal shield, parietal shield to postparietal shield, preorbital skull to postorbital skull, and the ratio of mandible height to mandible length. The fin characters are a first dorsal fin cranial to the pelvic fins and a second dorsal fin opposite the anal fin. This diagnosis demonstrates the continuing difficulty in identifying discrete autapomorphies for *Eusthenopteron*, even through the present.

Borgen and Nakrem (2016) provide a 14-character diagnosis of *Eusthenopteron*; however, many of these are listed as common or necessarily present in the taxon but not sufficient to diagnose a specimen to the taxon. Only two characters are listed as "possibly sufficient": both premaxillary and dental teeth exhibit a gradual increase in size at the symphysis (Borgen and Nakrem, 2016:448). Doubt over the sufficiency of these characters results from unclear conditions in *S. buetleri* and the species of *Platycephalichthys*. None of these species possess premaxillary tusks or dentary fangs; this improves the likelihood of their exhibiting gradually enlarged marginal teeth on

those elements (Borgen and Nakrem, 2016). Borgen and Nakrem (2016) additionally present a combination of features as "apparently a necessary and sufficient" character for *Eusthenopteron*: a parietal to postparietal shield ratio of 1.8–1.9 and a pineal opening at parietal midlength and in line with the rostral end of the postorbital.

Eusthenopteron is the best taxonomic grouping for the new species described here. In an effort to assign the new species confidently given the troubled taxonomic tradition of *Eusthenopteron*, we present a new diagnosis. "*Eusthenopteron*" applies to a tristichopterid with the following combination of features: two fang pairs on the third coronoid and no symphyseal dentary fang. No autapomorphy has yet been discovered for *Eusthenopteron*. Despite this, we believe that the above diagnosis improves the taxonomic status of the grouping. First, by focusing on characteristics of the tooth rows, the two included features are commonly preserved in material that is identifiably tristichopterid. Second, previous diagnoses have relied heavily on anatomical shapes and positions that may vary within the group and are additionally susceptible to specimen preservation and sample size. Both features of the above diagnosis are discrete. The new diagnosis, then, is better equipped to weather future discoveries that might influence the known variation for the group. It also makes the taxon easier to assess, regardless of specimen deformation. Additional work is required, although beyond the scope of the present work, to consider the species diagnoses of the now seven recognized species of *Eusthenopteron*. Our revised diagnosis for the group and needed work on the species themselves can allow *Eusthenopteron* to play a more important role in future systematic efforts focused on Tristichopteridae or Osteolepiformes.

ACKNOWLEDGMENTS

We thank C F. Mullison and B. Masek for fossil preparation; S. Bunson for photography, illustrations, and figure compilation; and K. Rozanitis and J. Stefl for curatorial support. G. Clement, Muséum National d'Histoire Naturelle; B. P. Kear, Museum of Evolution, Uppsala University; H. A. Nakrem, Natural History Museum, University of Oslo; and L. Werdelin, Swedish Museum of Natural History, provided useful information on historical specimens. D. Snitting made his dissertation work available to us. Relevant anatomical data were collected by a group of undergraduate students and we thank A. DeWitt, K. Kramer, and M. Wee, Swarthmore College, and S. Oswalt, Delaware Valley University, for their efforts to describe the *E. jenkinsi* referred material. We thank the Nunavut Ministry of Culture, Language, Elders, and Youth and the Grise Fiord Hamlet and Hunters and Trappers Association for providing permits that made this research possible. The Polar Continental Shelf Project provided logistical support, and the Canadian Museum of Nature provided collections support. The authors recognize everyone who has provided field assistance on the Nunavut Paleontological Expeditions (1999–2014). This research was supported by two anonymous donors; the Academy of Natural Sciences of Philadelphia; the Putnam Expeditionary Fund (Harvard University); the University of Chicago; the National Science Foundation grants EAR 0207721 (EBD), EAR 0544093 (EBD), EAR 0208377 (NHS), and EAR 0544565 (NHS); and the National Geographic Society Committee for Research and Exploration grants 7223-02, 7665-04, 8040-06, and 8420-08.

LITERATURE CITED

- Ahlberg, P. E., and Z. Johanson. 1997. Second tristichopterid (Sarcopterygii, Osteolepiformes) from the Upper Devonian of Canowindra, New South Wales, Australia, and phylogeny of the Tristichopteridae. *Journal of Vertebrate Paleontology* 17: 653–673.
- Ahlberg, P. E., and Z. Johanson. 1998. Osteolepiforms and the ancestry of tetrapods. *Nature* 395: 792–794.
- Andrews, S. M., and T. S. Westoll. 1970. The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. *Transactions of the Royal Society of Edinburgh* 68: 207–329.
- Bishop, P. J. 2013. A second species of *Tristichopterus* (Sarcopterygii: Tristichopteridae), from the Upper Devonian of the Baltic Region. *Memoirs of the Queensland Museum, Nature* 56: 305–309.
- Borgen, U. J., and H. A. Nakrem. 2016. Morphology, phylogeny, and taxonomy of osteolepiform fish. *Fossil and Strata* 61: 1–514.
- Chi, B. I., and L. V. Hills. 1976. Biostratigraphy and taxonomy of Devonian megaspores, Arctic Canada. *Bulletin of Canadian Petroleum Geology* 24: 640–818.
- Clement, G. 2002. Large Tristichopteridae (Sarcopterygii, Tetrapodomorpha) from the Late Famennian Evieux Formation of Belgium. *Palaeontology* 45: 577–593.
- Cloutier, R. 1996. Taxonomic review of *Eusthenopteron foordi*. Pp. 271–284 in: H.-P. Schultze and R. Cloutier, editors. *Devonian Fishes and Plants of Miguasha, Quebec, Canada*. Munich: Verlag Dr. Friedrich Pfeil.
- Cope, E. D. 1889. Synopsis of the families of Vertebrata. *American Naturalist* 23: 843–877.
- Daeschler, E. B., N. H. Shubin, and F. A. Jenkins, Jr. 2006. A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. *Nature* 440: 757–763.
- Daeschler, E. B., and J. P. Downs. 2018. New description and diagnosis of *Hyneria lindae* (Sarcopterygii, Tristichopteridae) from the Upper Devonian Catskill Formation in Pennsylvania. *U.S.A Journal of Vertebrate Paleontology*. DOI: 10.1080/02724634.2018.1448834.
- Downs, J. P., E. B. Daeschler, N. H. Shubin, and F. A. Jenkins, Jr. 2008. The cranial endoskeleton of *Tiktaalik roseae*. *Nature* 455: 925–929.
- Downs, J. P., E. B. Daeschler, F. A. Jenkins, Jr., and N. H. Shubin. 2011. A new species of *Laccognathus* (Sarcopterygii, Porolepiformes) from the Late Devonian of Ellesmere Island, Nunavut, Canada. *Journal of Vertebrate Paleontology* 31: 981–996.
- Downs, J. P., E. B. Daeschler, F. A. Jenkins, Jr., and N. H. Shubin. 2013. *Holoptychius bergmanni* sp. nov. (Sarcopterygii, Porolepiformes) from the Upper

- Devonian of Nunavut, Canada, and a review of *Holoptychius* taxonomy. *Proceedings of the Academy of Natural Sciences of Philadelphia* 162: 47–59.
- Egerton, P. M. G. 1861. *Tristichopterus alatus*. *Memoirs of the Geological Survey of the United Kingdom* 10: 51–55.
- Embry, A. F. 1988. Middle–Upper Devonian sedimentation in the Canadian Arctic Islands and the Ellesmerian Orogeny. Pp. 15–28 in: N. J. McMillan, A. F. Embry, and D. J. Glass, editors. *Canadian Society of Petroleum Geologists Memoir* 14(2). Calgary: Canadian Society of Petroleum Geologists.
- Embry, A. F. 1991. Middle–Upper Devonian clastic wedge of the Arctic islands. Pp. 263–279 in: H. P. Trettin, editor. *Geology of the Inuitian Orogen and Arctic Platform of Canada and Greenland*. Ottawa and Calgary: Geological Survey of Canada.
- Embry, A., and J. E. Klován. 1976. The Middle–Upper Devonian clastic wedge of the Franklinian Geosyncline. *Bulletin of Canadian Petroleum Geology* 24: 485–639.
- Jarvik, E. 1937. On the species of *Eusthenopteron* found in Russia and the Baltic States. *Bulletin of the Geological Institution of the University of Upsala* 27: 63–127.
- Jarvik, E. 1942. On the structure of the snout of crossopterygians and lower gnathostomes in general. *Zoologiska bidrag från Uppsala* 21: 235–675.
- Jarvik, E. 1944a. On the dermal bones, sensory canals and pitlines of the skull in *Eusthenopteron foordi* Whiteaves, with some remarks on *E. säve-söderberghi* Jarvik. *Kungliga Svenska Vetenskapsakademiens Handlingar* 21(3): 1–48.
- Jarvik, E. 1944b. On the exoskeletal shoulder-girdle of teleostomian fishes, with special reference to *Eusthenopteron foordi*. *Kungliga Svenska Vetenskapsakademiens Handlingar* 21(7): 1–32.
- Jarvik, E. 1952. On the fish-like tail in the ichthyostegid stegocephalians with descriptions of a new stegocephalian and a new crossopterygian from the Upper Devonian of East Greenland. *Meddelelser om Grönland* 114: 1–90.
- Jarvik, E. 1954. On the visceral skeleton in *Eusthenopteron* with a discussion of the parasphenoid and palatoquadrate in fishes. *Kungliga Svenska Vetenskapsakademiens Handlingar* 5(1): 1–104.
- Jarvik, E. 1980. *Basic Structure and Evolution of Vertebrates*. Volume 1. London: Academic Press.
- Jarvik, E. 1985. Devonian osteolepiform fishes from East Greenland. *Meddelelser om Grönland, Geoscience* 13: 1–52.
- Jarvik, E. 1996. The evolutionary importance of *Eusthenopteron foordi* (Osteolepiformes). Pp. 285–313 in: H.-P. Schultze and R. Cloutier, editors. *Devonian Fishes and Plants of Miguasha, Quebec, Canada*. Munich: Verlag Dr. Friedrich Pfeil.
- Johanson, Z. 2004. Late Devonian sarcopterygian fishes from eastern Gondwana (Australia and Antarctica) and their importance in phylogeny and biogeography. Pp. 287–308 in: G. Arratia, M. V. H. Wilson, and R. Cloutier, editors. *Recent Advances in the Origin and Early Radiation of Vertebrates*. Munich: Verlag Dr. Friedrich Pfeil.
- Johanson, Z., and P. E. Ahlberg. 1997. A new tristichopterid (Osteolepiformes: Sarcopterygii) from the Mandagery Sandstone (Late Devonian, Famennian) near Canowindra, NSW, Australia. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 88: 39–68.
- Johanson, Z., and A. Ritchie. 2000. Rhipidistians (Sarcopterygii) from the Hunter Siltstone (Late Famennian) near Grenfell, NSW, Australia. *Fossil Record* 3: 111–136.
- Johanson, Z., P. Ahlberg, and A. Ritchie. 2003. The braincase and palate of the tetrapodomorph sarcopterygian *Mandageria fairfaxi*: morphological variability near the fish-tetrapod transition. *Palaeontology* 46: 271–293.
- Kiaer, J. 1915. Upper Devonian fish remains from Ellesmere Land with remarks on *Drepanaspis*. *Report of the Second Norwegian Arctic Expedition in the "Frau" 1898–1902*, 33: 1–53.
- Long, J. A. 1985. The structure and relationships of a new osteolepiform fish from the Late Devonian of Victoria, Australia. *Alcheringa* 9(1): 1–22.
- Mayr, U. 1994. Regional geology. Pp. 12–16 in: U. Mayr, J. J. Puckard, Q. H. Goodbody, A. V. Okulitch, R. J. Rice, F. Goodarzi, and K. R. Stewart, editors. *The Phanerozoic Geology of Southern Ellesmere and North Kent Islands, Canadian Arctic Archipelago*. Ottawa and Calgary: Geological Survey of Canada.
- Miller, J. H., N. Shubin, E. Daeschler, and J. Downs. 2007. Stratigraphic context of *Tiktaalik roseae* (Late Devonian): paleoenvironment of the fish-tetrapod transition. Geological Society of America Meeting: 28–31 October 2007; Denver, Colorado. *Abstracts and Programs* 39: 417.
- Orvig, T. 1957. Remarks on the vertebrate fauna of the Lower Upper Devonian of Escuminac Bay, P.Q., Canada, with special reference to the Porolepiform Crossopterygians. *Arkiv För Zoologi* 10: 367–426.

- Parfitt, M., Z. Johanson, S. Giles, and M. Friedman. 2014. A large, anatomically primitive tristichopterid (Sarcopterygii: Tetrapodomorpha) from the Late Devonian (Frasnian) Alves Beds, Upper Old Red Sandstone, Moray, Scotland. *Scottish Journal of Geology* 50(1): 79–85.
- Porro, L. B., E. J. Rayfield, and J. A. Clack. 2015. Computed tomography, anatomical description, and three-dimensional reconstruction of the lower jaw of *Eusthenopteron foordi* Whiteaves, 1881 from the Upper Devonian of Canada. *Palaeontology* 58: 1031–1047.
- Rohon, J. V. 1889. Die Dendrodonten des devonischen systems in Russland. *Mémoires de l'Académie Impériale des Sciences de St. Petersburg VII*, 36(14): 1–52.
- Scotese, C. R., and W. S. McKerrow. 1990. Revised world maps and introduction. *Geological Society, London, Memoirs* 12: 1–21.
- Shubin, N. H., E. B. Daeschler, and F. A. Jenkins, Jr. 2006. The pectoral fin of *Tiktaalik roseae* and the origin of the tetrapod limb. *Nature* 440: 764–771.
- Shubin, N. H., E. B. Daeschler, and F. A. Jenkins, Jr.. 2015. Origin of the tetrapod neck and shoulder. Pp. 63–76 in: K. Dial, N. Shubin, and E. Brainerd, editors. *Great Transformations in Vertebrate Evolution*. Chicago: University of Chicago Press.
- Smithson, T. R., and K. S. Thomson. 1982. The hyomandibular of *Eusthenopteron foordi* Whiteaves (Pisces: Crossopterygii) and the early evolution of the tetrapod stapes. *Zoological Journal of the Linnean Society* 74: 93–103.
- Snitting, D. 2008. A redescription of the anatomy of the Late Devonian *Spodichthys buetleri* Jarvik, 1985 (Sarcopterygii, Tetrapodomorpha) from East Greenland. *Journal of Vertebrate Paleontology* 28: 637–655.
- Snitting, D. 2009. *Heddeleithys*—a new tristichopterid genus from the Dura Den Formation, Midland Valley, Scotland (Famennian, Late Devonian). *Acta Zoologica* 90(Supplement 1): 273–284.
- Swartz, B. 2012. A marine stem-tetrapod from the Devonian of western North America. *PLoS ONE* 7(3): e33683.
- Traquair, R. H. 1875. On the structure and affinities of *Tristichopterus alatus*, Egerton. *Transactions of the Royal Society of Edinburgh* 27: 383–396.
- Traquair, R. H. 1890. Notes on the Devonian fishes of Scaumenac Bay and Campbelltown in Canada. *Geological Magazine* 7(1): 15–22.
- Vorobyeva, E. I. 1962. Rhizodont crossopterygian fishes from the main Devonian field of the USSR. *Trudy Paleontologicheskogo Instituta* 94: 1–140. [In Russian]
- Vorobyeva, E. I. 1977. Morphology and peculiarities of evolution in crossopterygian fish. *Trudy Paleozoologicheskogo Instituta* 163: 1–239. [In Russian]
- Vorobyeva, E. I., and D. V. Obruchev. 1964. Podklass Sarcopterygii. Pp. 68–109 in: D. V. Obruchev, editor. *Osnovy paleontologii*, Vol. XI. *Agnatha, Pisces*. Moscow: Izdatel'stvo "NAUKA." [In Russian]
- Westoll, T. S. 1937. On a specimen of *Eusthenopteron* from the Old Red Sandstone of Scotland. *Geological Magazine* 74: 507–524.
- Westoll, T. S. 1940. New Scottish material of *Eusthenopteron*. *Geological Magazine* 77: 65–73.
- Westoll, T. S. 1943. The hyomandibular of *Eusthenopteron* and the tetrapod middle ear. *Proceedings of the Royal Society of London, Series B* 131: 393–414.
- White, E. I. 1961. The Old Red Sandstone of Brown Clee Hill and the adjacent area. Part II. Palaeontology. *Bulletin of the British Museum of Natural History, Geology*, 5: 243–310.
- Whiteaves, J. F. 1881. On some remarkable fossil fishes from the Devonian rocks of Scaumenac Bay, in the Province of Quebec. *American Journal of Science* 21: 494–496. [Reprinted in *Annals and Magazine of Natural History* 8: 159–162]
- Whiteaves, J. F. 1883. On some remarkable fossil fishes from the Devonian rocks of Scaumenac Bay, P.Q., with descriptions of a new genus and three new species. *The Canadian Naturalist and Quarterly Journal of Science*, 10(1): 27–35.
- Whiteaves, J. F. 1889. Illustrations of the fossil fishes of the Devonian rocks of Canada. Part II. *Proceedings and Transactions of the Royal Society of Canada* 6(4): 77–96.
- Young, B., R. L. Dunstone, T. J. Senden, and G. C. Young. 2013. A gigantic sarcopterygian (tetrapodomorph lobe-finned fish) from the Upper Devonian of Gondwana (Eden, New South Wales, Australia). *PLoS ONE* 8(3): e53871.
- Young, G. C., J. A. Long, and A. Ritchie. 1992. Crossopterygian fishes from the Devonian of Antarctica: systematics, relationships and biogeographic significance. *Records of the Australian Museum* 14(Supplement): 1–77.
- Zupinš, I. 2008. A new tristichopterid (Pisces, Sarcopterygii) from the Devonian of Latvia. *Proceedings of the Latvian Academy of Sciences* 62: 40–46.